



# Detection of flickering edges: absence of a red–green edge detector

P.D. Gowdy<sup>a,b</sup>, C.F. Stromeyer III<sup>b,\*</sup>, R.E. Kronauer<sup>b</sup>

<sup>a</sup> *Department of Psychology, Harvard University, Cambridge, MA 02138, USA*

<sup>b</sup> *Division of Engineering and Applied Sciences, Harvard University, Cambridge, MA 02138, USA*

Received 22 July 1998; received in revised form 17 May 1999

## Abstract

Kelly ((1975) *Science*, 188, 371–372) showed that a centrally-fixated, contrast-reversing edge has a very different effect on the detection of luminance and red–green flicker. Red–green flicker sensitivity was  $\sim 3$ -fold greater for a uniform field than for a ‘split’ field with the two sides flickering out-of-phase. Just the opposite effects were observed for luminance flicker — the split field yielded a 7-fold advantage over the uniform field at 2 or 4 Hz and a 3-fold advantage at 12 Hz. Contrary to Kelly, we find that the split field offers only a very small advantage of 40% for luminance flicker at 2 Hz and virtually no advantage at 4 Hz and above. Kelly’s chromatic results are surprising since one might expect that the larger color difference (or step) across the central edge would aid chromatic discrimination rather than strongly suppressing sensitivity. We show that the central chromatic edge only weakly impairs detection. Further results show that the two sides of the chromatic split field are detected essentially independently by red or green ‘blob’ detectors, which do not take advantage of the color difference *across* the edge. This has a remarkable implication: when wavelength discrimination is measured with a bipartite field whose two side are slowly modulated in opposite directions, then one side may be deleted with little adverse effect. © 1999 Elsevier Science Ltd. All rights reserved.

**Keywords:** Red–green mechanism; Luminance mechanism; Flicker; Edge detector

## 1. Introduction

In a widely cited study Kelly (1975) showed that a central contrast-reversing edge has very different effects on detection of luminance (LUM) and red–green (RG) chromatic flicker. Flicker was presented in a centrally-fixated,  $10^\circ$  yellow field of 1000 td (Fig. 1) with dark surround. For uniform field flicker, LUM sensitivity decreased strongly at low temporal frequencies, but when the field was split so that the two sides flickered out-of-phase, LUM sensitivity increased by 7-fold at 2 and 4 Hz and  $\sim 3$ -fold at 12 Hz. The opposite effect was observed with RG flicker: changing from a uniform field to the split field suppressed sensitivity by a large factor of 3-fold at 2 Hz and by 2-fold at 12 Hz.

Kelly (1975) explained these edge effects by a spatial inhibitory (gain control) process which operated *between* the L and M cone signals and was common to the LUM and RG pathways. The gain control was assumed to be temporally low-pass, so the edge effects

would fall-off with increasing temporal frequency but still be clearly present at 12 Hz. In this gain control process, the L and M cone signals antagonize each other when stimulated in phase. Thus for uniform LUM flicker, the gain control counteracts the intensity variations at low temporal frequencies and reduces sensitivity, while the contrast-reversing LUM edge attenuates the inhibition process, thereby increasing sensitivity. For the uniform RG flicker, the L and M signals are out-of-phase; this also reduces the inhibition and enhances sensitivity. However, for the split red–green field the L and M cones signals are in phase across the edge, thus antagonizing each other and reducing sensitivity. Other explanations of the edge effects are considered in Section 4.

The edge effects observed by Kelly are surprisingly large. Kelly (1975) employed the method of adjustment and did not state what cues were used to detect the flicker. We have reexamined these effects, using a forced-choice method.

We were particularly intrigued by Kelly’s finding that the central red–green edge produces such a large suppression. One might initially surmise that the substan-

\* Corresponding author. Fax: +1-617-495-9837.

E-mail address: charles@stokes.harvard.edu (C.F. Stromeyer)

tial color difference *across* the edge would aide chromatic detection, since the difference between the two sides of the field might be more readily compared. That is, when one side of the split field reaches its red–most excursion, the other side is at its green–most excursion. This results in a large chromatic difference across the central edge. Our measurements provide an explanation of why the edge does not help. It is also unclear why the split field would produce such strong suppression, since color mechanisms situated slightly away from the edge would be well stimulated by locally uniform regions of the field.

## 2. Methods

### 2.1. Stimuli and apparatus

We used a test field of  $3.5^\circ$  diameter, whereas Kelly used a  $10^\circ$  field. Our smaller field reduces the effects of retinal inhomogeneity and assures foveal processing. The test stimuli were generated on red and green CRT monitors (Tektronix 608) which were optically filtered and combined with a dichroic mirror (Stromeyer, Kronauer, Ryu, Chaparro & Eskew, 1995). This test was superposed on an uniform  $4.2^\circ$  dia field (in Maxwellian view) of 562 nm and 1000 td, rendering the test region metameric to 566 nm and 1600 td. This yellowish field largely eliminates temporal phase shifts between the L and M signals in the LUM mechanism, thus better isolating the LUM and RG mechanisms; such phase shifts are nil in the RG mechanism (Stromeyer, Chaparro, Tolia & Kronauer, 1997).

The display was monocularly viewed through a 3 mm artificial pupil and lens that corrects for ocular chromatic aberration (Powell, 1981). Observers were re-

fracted with a spectacle lens mounted against this achromatizing lens, and the head was immobilized with a bite bar.

The spectral radiance of the red and green lights were calibrated at the eyepiece at 1 nm intervals with a radiometer and monochromator (2 nm HBW). These spectral radiances were then weighted by the Smith and Pokorny (1975) cone spectral sensitivities to calculate cone contrast. Stimuli are represented as vectors in the  $L', M'$  cone contrast plane.  $M'$  cone contrast is defined as  $M' = \Delta M/M$ , where  $\Delta M$  is M cone stimulation attributable to the amplitude of the test stimulus and  $M$  is the mean M cone stimulation owing to the entire field. L cone contrast,  $L'$ , is defined in a similar manner. The overall contrast is specified by the vector length,  $VL = (L'^2 + M'^2)^{1/2}$ , in this plane — the *one-sided* length from the origin to the tip of the vector.

The LUM stimulus is a  $45\text{--}225^\circ$  vector in the  $L', M'$  plane, having the *same* color as the field. The equiluminant RG direction is a vector of  $112\text{--}292^\circ$ , assessed with the quadrature motion paradigm (Stromeyer et al., 1995).

### 2.2. Procedure

Thresholds were measured with a forced-choice procedure. Each trial contained two temporal intervals, separated by 200 ms, with the flicker presented in one interval chosen randomly. The flicker was ramped on for 125 ms with a raised cosine envelope, held constant for 500 ms and then ramped off (the envelope was expanded 2-fold for the lowest frequency of 2 Hz). Tones signaled each interval and provided feedback. Each run employed a single temporal frequency of the LUM or RG flicker, with the uniform and split field conditions randomly intermixed, within separate staircases. Test contrast was changed in 0.1 log unit steps with 12-bit digital-to-analog converters. The staircase estimated threshold at the 71% detection level, with each threshold typically based on 5–10 runs.

## 3. Results

### 3.1. Flicker sensitivity

Fig. 2 shows contrast sensitivity for LUM and RG flicker in the uniform field (circles) and split field (squares). Sensitivity is defined as the reciprocal of threshold vector length.

The LUM sensitivity is band-pass, peaking near 8 Hz (Kelly, 1975). Consistent with Kelly (1975), LUM sensitivity at 2 Hz is greater for the split field than for the uniform field. However, we find only a 40% advantage compared to Kelly's 7-fold advantage. The LUM sensitivity from 4 to 12 Hz is nearly the *same* for the

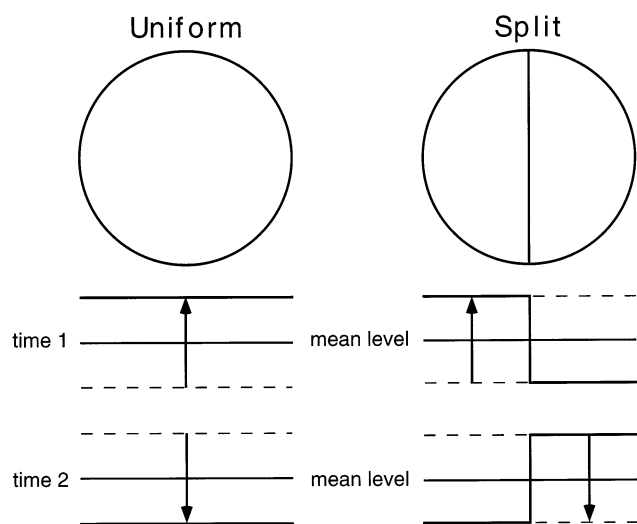


Fig. 1. Profile of the uniform field and the split field, whose two sides flicker out-of-phase. Contrast is shown equated for the two fields.

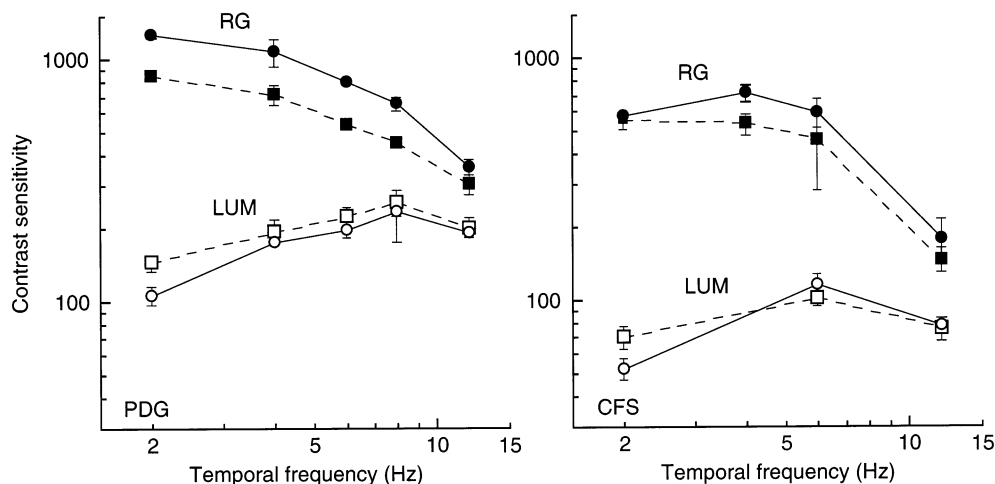


Fig. 2. Temporal contrast sensitivity functions for RG and LUM flicker, measured with a uniform field (circles) and a split, counterphase field (squares). Error bars represent  $\pm 1$  S.E.M.

uniform and split fields, whereas Kelly observed that the split field provided an advantage of 7-fold at 4 Hz which declined to 3-fold at 12 Hz. Our observers reported that the LUM flicker appeared essentially identical within the uniform and split field; thus it was difficult to discern that the two sides of the split field flickered out-of-phase.

Sensitivity is higher for the RG flicker than the LUM flicker over the entire range of 2–12 Hz consistent with earlier results (Stromeyer, Cole & Kronauer, 1987), thus demonstrating that the RG flicker is not detected by intrusion of the LUM mechanism. The RG flicker shows the typical low-pass temporal characteristic (Kelly, 1975). Like Kelly (1975) we find that sensitivity is reduced for the split field compared to the uniform field, but fail to replicate the 3-fold disadvantage observed by Kelly. For observer CFS, the chromatic edge worsens detection by only 30% from 4 to 12 Hz and the effect largely disappears at 2 Hz. For observer PDG the edge reduces sensitivity by  $\sim 55\%$  at all temporal frequencies. The RG flicker appeared essentially identical within the uniform and split fields, and it was difficult to discern that the two sides flickered out-of-phase. The color flicker was most apparent at a distance slightly away from the central edge.

In summary, our results are in the direction of Kelly's (1975) but the effects are much weaker.

### 3.2. Absence of RG edge detection

We initially surmised that the color difference across the central edge of the split field might help chromatic discrimination or detection. The weakly adverse effect of the edge might be explained as follows. The most sensitive color detectors may be spatially low-pass 'blob' detectors, responding best to spatially uniform red or green shifts (Gowdy, Stromeyer & Kronauer,

1999). For the split field, response cancellation would occur in those blob detectors aligned along the central edge, since the edge is red and green to either side. This region includes the central fovea where color sensitivity is highest (Mullen, 1991). RG sensitivity may fall quickly away from central fovea; for example, the threshold for a red or green chromatic flash ( $1^\circ$ , 200 ms) rises 3–4-fold when the flash is moved outward only  $2.3^\circ$  from fixation (Stromeyer, Lee & Eskew, 1992). Thus response cancellation within the central, *most-sensitive* blob detectors may yield a slightly weaker response for the split field. Hence, the best-stimulated blob detectors may lie slightly to either side of the central edge.

We now test whether the two sides of the chromatic split field are detected independently. Fig. 3 shows the three stimuli we compared: a split red–green field (a bipolar pattern), a red-sided field or a green-sided field

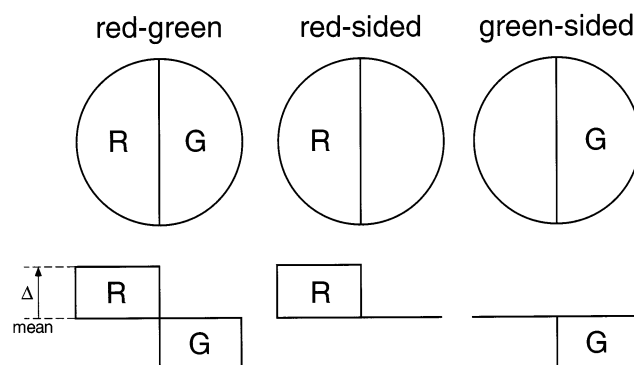


Fig. 3. Spatial profiles of static RG patterns used for results in Fig. 4: bipolar red–green pattern, unipolar red-sided pattern and unipolar green-sided pattern. The three patterns are depicted with equal contrast — where contrast is defined to be proportional to  $\Delta/\text{mean}$  (the amplitude of the stimulus divided by the mean level). But the 'edge-contrast' (proportional to the height across the edges) is twice as great for the bipolar pattern.

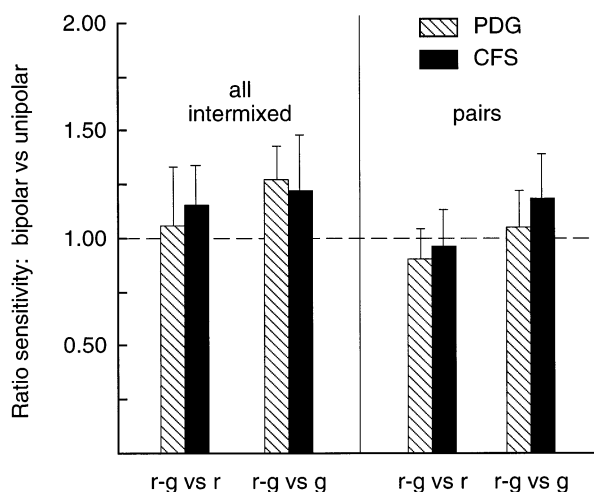


Fig. 4. Ratio of sensitivity of the bipolar and unipolar RG patterns in Fig. 3. A ratio of 1.0 would mean that the three patterns in Fig. 3 are equally detectable. In individual runs the bipolar pattern was intermixed with both unipolar patterns (left panel) or with just the green or red unipolar pattern (right panel). Error bars represent  $\pm 1$  S.E.M.

(unipolar patterns, consisting of just one side of the bipolar pattern). The stimuli were not flickered but presented statically, being ramped on for 95 ms with a raised cosine, held steady for 379 ms and then ramped off. Between trials the left and right sides were randomly reversed. Measurements were collected in two ways: the three stimuli were randomly intermixed within each run, or the red–green pattern was randomly paired with just the green-sided or the red-sided pattern.

The three stimuli in Fig. 3 are depicted with equal contrast — where contrast is defined as the amplitude of the stimulus divided by the mean level (Section 2). If the red and green regions are detected separately, then contrast sensitivity should be similar for the three patterns (although probability summation may yield a slight advantage for the red–green pattern — discussed below). Fig. 4 shows that the ratio of contrast sensitivity is nearly 1.0 for the bipolar pattern versus unipolar patterns; thus the three patterns are about equally detectable.

Probability summation amongst spatially independent blob detectors might be expected to slightly increase sensitivity to the bipolar pattern relative to the unipolar patterns, since the bipolar pattern has both a red and a green side. Following Mullen, Cropper and Losada (1997), we can estimate the role of probability summation by the formula:

$$S^k = S_R^k + S_G^k \quad (1)$$

where  $S$  is the overall contrast sensitivity,  $S_R$  and  $S_G$  are the sensitivities of the red and green blob detectors (assumed to be equal) and  $k$  is the slope of the psychometric function. For detection of static RG stimuli the

slope varies from about 2 (Cole, Stromeyer & Kronauer, 1990) to 4 (Cole, Hine & McIlhagga, 1993). Thus probability summation predicts an advantage of  $\sim 19$ –41% for the bipolar pattern. The measured advantage (Fig. 4) for the bipolar pattern generally falls below this range. This shortfall might be caused by the bipolar pattern producing inhibition in blob detectors centered on the red–green edge, as described above.

When these patterns are equated in contrast (as in Fig. 3), the contrast *across* the edge (or ‘edge-contrast’) is twice as great for the bipolar pattern compared to the unipolar patterns. But this greater difference is not reflected in detection performance. The results thus suggest that the two sides are separately processed by chromatic blob detectors.

The results were very different for similar, static LUM patterns. Measurements were repeated with LUM patterns analogous to those shown in Fig. 3. In individual runs a split light–dark field was intermixed with a light-sided only field or a dark-sided only field. Contrast sensitivity for the light–dark pattern was roughly twice that for the one sided patterns (ratios of 2.2 and 2.3, observer CFS). Thus the edge-contrast controls detection of these static luminance patterns.

## 4. Discussion

### 4.1. Detection of the LUM flicker

In general we replicate the trends of Kelly (1975), but our effects are much smaller.

For LUM flicker at 2 Hz, we observed that the central edge provides only a 40% advantage, compared to the 7-fold advantage observed by Kelly. From 4 to 12 Hz, we observed that LUM sensitivity was unaffected by the central flickering edge, whereas Kelly found that the edge improved sensitivity by 7- to 3-fold over this range. The similarity we observe for the two conditions suggests that at these higher temporal frequencies the flicker is detected by flicker or motion detectors sensitive to rather low spatial frequencies (King-Smith & Kulikowski, 1975; Kelly, 1979). Robson (1966) observed that sensitivity to low *spatial* frequencies is enhanced by raising temporal frequency. Similar effects are evident at the retinal ganglion cells, as shown in cat (Enroth-Cugell, Robson, Schweitzer-Tong & Watson, 1983).

In summary, our LUM flicker data show a very weak effect of the central reversing edge, unlike the large effects of Kelly. This difference cannot be explained by our smaller field ( $3.5^\circ$ ), for the low-frequency decline in temporal sensitivity is very similar for  $4^\circ$  and  $65^\circ$  uniform fields (Kelly, 1959; Keesey, 1970). Also, our results and Kelly’s (1975) show an *equivalent* low-frequency drop in sensitivity to uniform flicker

between 6 and 2 Hz. Nor can the difference be explained by our background field extending slightly beyond the test region, since deleting this region had no effect (as shown by results for observer PDG at 2 Hz).

At very low temporal frequencies the central LUM edge is important. The luminance contrast *across* the central edge (the edge-contrast) determined the detectability of our *static* unipolar and bipolar LUM edges. These static stimuli are likely detected by the ‘sustained’ channels (Kulikowski & Tolhurst, 1973). Kulikowski and Tolhurst observed a very similar effect using a ‘pattern’ detection criterion to isolate the ‘sustained’ channels: contrast thresholds were the same for gratings which were counterphased (with a temporal square-wave) versus switched on and off at 3.5 Hz. This equates the static ‘edge-contrast’ of the two patterns, although the counterphase pattern produces twice as large luminance changes at the moment of switching. The ‘transient’ detectors are sensitive to these latter changes, whereas the sustained detectors are sensitive to the static edge-contrast.

#### 4.2. Detection of the RG flicker and chromatic blob detectors

For RG flicker, the central contrast-reversing edge slightly suppressed detection by 30–55% for our two observers — much less than the 3-fold effect of Kelly. The weak suppression might be caused by inhibition in sensitive chromatic blob detectors lying on the central red–green edge.

Evidence for these blob detectors was provided by our results showing a similar detectability for the static bipolar red–green field and either of its two sides alone. Gowdy et al. (1999) measured similar effects with low spatial frequency gratings. These results suggest that the red and green regions of spatially coarse stimuli may be detected separately, agreeing with the recent conclusion of Zaidi, Spehar and DeBonet (1997).

The chromatic blob detectors are assumed to be essentially low-pass spatial filters with poor spatial tuning. Nevertheless the blob detectors may convey information about spatial position, since there may be an array of such detectors signaling different spatial positions. However, spatially-tuned (band-pass) RG mechanisms have been revealed in studies on spatial adaptation (Bradley, Switkes & De Valois, 1988), masking (De Valois & Switkes, 1983) and pattern discrimination (Webster, De Valois & Switkes, 1990). The overall spatial contrast sensitivity function for RG is low-pass (Mullen, 1985), but Losada and Mullen (1994) have argued that this function may represent the envelope of a range of spatial band-pass mechanisms, since spatial masking reveals the presence of band-pass mechanisms tuned as low as 0.25–1 cpd (although the bandwidths are very broad). This finding however does not neces-

sarily rule out the blob detectors as being the most sensitive mechanisms for detecting coarse colored features, for the spatial adaptation paradigm (and, by extension, the masking paradigm) are biased to reveal the most spatially-tuned mechanisms (Bradley et al., 1988).

The postulated blob detectors may have an approximately unipolar *spatial* receptive field. However, their *response* may be bipolar in the sense of being equally sensitive to red or green uniform shifts. Calkins, Thornton and Pugh (1992) provide reasons for postulating such bipolar response mechanisms, rather than distinct mechanisms for detecting red changes versus green changes. However there is some evidence for unipolar response mechanisms, sensitive to the *direction* of color change in a uniform field (Zaidi and Halevy, 1993).

In summary, the red and green regions of spatially coarse stimuli may be detected separately by the sensitive blob detectors. This has a remarkable implication. Wavelength discrimination is often measured with a bipartite field whose two sides are slowly deviated in opposite directions. The discrimination threshold may be little affected by eliminating one side of the field, since the most-sensitive chromatic detectors do not use the information across the chromatic border.

#### 4.3. Effect of coincident luminance edge on detection of red–green edge

The RG split field may be detected by blob detectors which are insensitive to the central red–green edge. However, briefly adding a clearly visible LUM edge to the chromatic edge allows the RG mechanism to detect the chromatic *difference* across the edge (Gowdy et al., 1999). The LUM edge may facilitate detection of spatially coarse RG patterns by as much as 5–7-fold (Gowdy et al., 1999). Part of this large facilitation can be ascribed to the fact that the LUM edge makes the RG mechanism sensitive to the difference across the red–green edge, whereas without the LUM edge the red and green areas are detected largely independently, so that the red–green edge is not effectively utilized.

#### Acknowledgements

We thank E. Switkes for comments. Research supported by NIH EY11246.

#### References

- Bradley, A., Switkes, E., & De Valois, K. (1988). Orientation and spatial frequency selectivity of adaptation to color and luminance gratings. *Vision Research*, 28, 841–856.

- Calkins, D. J., Thornton, J. E., & Pugh, E. N. Jr. (1992). Monochromatism determined at a long-wavelength/middle-wavelength cone-antagonistic locus. *Vision Research*, 32, 2349–2367.
- Cole, G. R., Hine, T., & McIlhagga, W. (1993). Detection mechanisms in L-, M-, and S-cone contrast space. *Journal of the Optical Society of America A*, 10, 38–51.
- Cole, G. R., Stromeyer, C. F. III, & Kronauer, R. E. (1990). Visual interactions with luminance and chromatic stimuli. *Journal of the Optical Society of America A*, 7, 128–140.
- De Valois, K. K., & Switkes, E. (1983). Simultaneous masking interactions between chromatic and luminance gratings. *Journal of the Optical Society of America*, 73, 11–18.
- Enroth-Cugell, C., Robson, J. G., Schweitzer-Tong, D. E., & Watson, A. B. (1983). Spatio-temporal interactions in cat retinal ganglion cells showing linear spatial summation. *Journal of Physiology*, 341, 279–307.
- Gowdy, P. D., Stromeyer III, C. F., & Kronauer, R. E. (1999). Facilitation between the luminance and red–green detection mechanisms: enhancing contrast differences across edges. *Vision Research*, 39, 4098–4112.
- Kelly, D. H. (1959). Effects of sharp edges in a flickering field. *Journal of the Optical Society of America*, 49, 730–732.
- Kelly, D. H. (1975). Luminous and chromatic flickering patterns have opposite effects. *Science*, 188, 371–372.
- Kelly, D. H. (1979). Motion and vision. II Stabilized spatio-temporal threshold surface. *Journal of the Optical Society of America*, 69, 1340–1349.
- Keesey, U. T. (1970). Variables determining flicker sensitivity in small fields. *Journal of the Optical Society of America*, 60, 390–398.
- King-Smith, P. E., & Kulikowski, J. J. (1975). Pattern and flicker detection analysed by subthreshold summation. *Journal of Physiology*, 249, 519–548.
- Kulikowski, J. J., & Tolhurst, D. J. (1973). Psychophysical evidence for sustained and transient detectors in human vision. *Journal of Physiology*, 232, 149–162.
- Losada, M. A., & Mullen, K. T. (1994). The spatial tuning of chromatic mechanisms identified by simultaneous masking. *Vision Research*, 34, 331–341.
- Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology*, 259, 381–400.
- Mullen, K. T. (1991). Colour vision as a post-receptoral specialization of the central visual field. *Vision Research*, 31, 119–130.
- Mullen, K. T., Cropper, S. J., & Losada, M. A. (1997). Absence of linear subthreshold summation between red–green and luminance mechanisms over a wide range of spatio-temporal conditions. *Vision Research*, 37, 1157–1165.
- Powell, I. (1981). Lens for correcting chromatic aberration of the eye. *Applied Optics*, 20, 4152–4155.
- Robson, J. G. (1966). Spatial and temporal contrast-sensitivity function of the visual system. *Journal of the Optical Society of America*, 56, 1141–1142.
- Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research*, 15, 161–171.
- Stromeyer, C. F. III, Chaparro, A., Tolias, A. S., & Kronauer, R. E. (1997). Colour adaptation modifies the long-wave *versus* middle-wave weights and temporal phases in human luminance (but not red–green) mechanism. *Journal of Physiology*, 499, 227–254.
- Stromeyer, C. F. III, Cole, G. R., & Kronauer, R. E. (1987). Chromatic suppression of cone inputs to the luminance flicker mechanism. *Vision Research*, 27, 1113–1137.
- Stromeyer, C. F. III, Kronauer, R. E., Ryu, A., Chaparro, A., & Eskew, R. T. Jr. (1995). Contribution of the long-wave and middle-wave cones to motion detection. *Journal of Physiology*, 485, 221–243.
- Stromeyer, C. F. III, Lee, J., & Eskew, R. T. Jr. (1992). Peripheral chromatic sensitivity for flashes: a post-receptoral red–green asymmetry. *Vision Research*, 32, 1865–1873.
- Webster, M. A., De Valois, K. K., & Switkes, E. (1990). Orientation and spatial-frequency discrimination for luminance and chromatic gratings. *Journal of the Optical Society of America A*, 7, 1034–1049.
- Zaidi, Q., & Halevy, D. (1993). Visual mechanisms that signal the direction of color changes. *Vision Research*, 33, 1037–1051.
- Zaidi, Q., Spehar, B., & DeBonet, J. (1997). Color constancy in variegated scenes: role of low-level mechanisms in discounting illumination changes. *Journal of the Optical Society of America A*, 14, 2608–2621.